

Dipodomys venustus. By Troy L. Best

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Dipodomys venustus (Merriam, 1904)

Santa Cruz Kangaroo Rat

Perodipus venustus Merriam, 1904:142. Type locality "Santa Cruz, Santa Cruz Co., California."

Dipodomys venustus: Grinnell, 1919:204. First use of current name combination.

Dipodomys sanctiluciae Grinnell, 1919:204. Type locality "ridge clothed with digger pine and chaparral, one mile southwest of Jolon, Monterey County, California."

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Dipodomysinae. A key to the 22 species of *Dipodomys* is presented in Best (1991). Two subspecies of *D. venustus* are recognized (Hall, 1981):

D. v. sanctiluciae Grinnell, 1919:204, see above.

D. v. venustus (Merriam, 1904:142), see above.

DIAGNOSIS. *Dipodomys venustus* (Fig. 1) occurs in or adjacent to the range of three other species of five-toed kangaroo rats: *D. agilis*, *D. elephantinus*, and *D. heermanni* (Hall, 1981). Compared with *D. agilis*, *D. venustus* has a much darker color, a slightly longer skull, a maxillary arch of the zygoma that is broader on the outer side with a pronounced outer angle (lacking in *D. agilis*), a weaker jugal, slightly longer and broader nasals, broader premaxillae, heavier incisors (Merriam, 1904), bolder facial markings, much larger ear, much longer tail, and a proportionally longer rostrum. In addition, the nasals average 15.6 mm in *D. venustus* compared with 14.3 mm in *D. agilis* (Grinnell, 1922) and the larger bullae of *D. agilis* give its skull a more triangular appearance in dorsal aspect than the skull of *D. venustus* (Boulware, 1943).

Compared with *D. elephantinus*, *D. venustus* is smaller, dark in color (especially the head, where the cheeks have less white, the ears are blacker, and the facial arietiform marking is bolder), and has weaker incisors, rostrum narrower at the end, bullae smaller, and interparietal and supraoccipital broader. The teeth of *D. venustus* are smaller and the ear is smaller, darker in color, and at most there may be a sparse sprinkling of white hairs on their inner surface (Grinnell, 1922). Also, the ear of *D. venustus* is mostly blackish rather than brownish, the length of ear is <16.5 mm rather than >16.5 mm, and the dark ventral tail stripe is wider than the lateral white stripe at mid-length of the tail, rather than the dark ventral tail stripe being narrower than the lateral white stripe (Ingles, 1965).

Compared with *D. heermanni*, the nasals and the premaxillae of *D. venustus* are broader, the outer angle of the maxillary arch is less developed, and the bullae project more posteriorly (Merriam, 1904). The most conspicuous differences are the darker coloration and the much larger ear of *D. venustus* (Grinnell, 1922).

GENERAL CHARACTERS. *Dipodomys venustus* is a narrow-faced (Fig. 2), five-toed kangaroo rat, with dark coloration (Grinnell, 1922). It is medium-sized for the genus (Best, in press). The nose is black, passing into a black band at the base of the whiskers. The top of the head, back, and thigh patches are dusky and finely grizzled with ochraceous, the ochraceous becoming more distinct on the sides. The ears are large and nearly black, with pale spots at the base and at the top of the fold. The ankle, sides of the heel, sole, and tail stripes are nearly black. The hairs of the rump form a black patch just in front of the basal white ring of the tail (Merriam, 1904). *D. v. sanctiluciae* is paler in color, the pale areas on the cheek and between the eye and ear are paler, there are more of the rather long white hairs on the inner surface of the pinna, and there is greater inflation of the mastoid bullae than in *D. v. venustus* (Grinnell, 1922).

The length of hind foot is 38% of the length of head and body and the tail is 159% of the length of head and body (Hatt, 1932). Mean measurements (in mm) of 65 adult males and 73 adult females,

respectively, from throughout the range of the species are: total length, 318.2, 313.5; length of body, 128.7, 122.9; length of tail, 192.9, 190.7; length of hind foot, 45.8, 45.1; length of ear, 18.6, 18.2; basal length of cranium, 23.6, 23.3; greatest length of cranium, 41.6, 41.0; maxillary arch spread, 22.1, 21.7; interorbital width, 11.0, 11.0; nasal length, 15.6, 15.4; intermaxillary width, 7.7, 7.6; alveolar length, 5.3, 5.3; lacrimal length, 3.8, 3.7; maxillary arch width, 5.3, 5.2; basioccipital length, 6.0, 6.0; greatest depth of cranium, 13.7, 13.5; greatest width of cranium, 25.1, 24.7; zygomatic width, 20.6, 19.9; and nasal width, 4.2, 4.2 (Best, in press). Mass for a male and female, respectively, is 82.0 and 87.7 g (Grinnell, 1922).

Of 19 morphologic characters, nine exhibit significant sexual dimorphism in size. Males are significantly larger than females in total length, length of hind foot, basal length of cranium, greatest length of cranium, maxillary arch spread, width of maxillary arch, greatest depth of cranium, greatest width of cranium, and zygomatic width (Best, in press).

DISTRIBUTION. The Santa Cruz kangaroo rat occurs along the coastal mountains of west-central California (Fig. 3). It inhabits slopes clothed with chaparral or a mixture of chaparral and oaks (*Quercus*) or digger pine (*Pinus*; Grinnell, 1933). The altitudinal range is from sea level to 1,770 m (Grinnell, 1922). No fossils of *D. venustus* are known.

FORM AND FUNCTION. *Dipodomys venustus* is adapted for ricochetal locomotion (Hatt, 1932). The distal 4 mm of the dorsal guard hairs are darkly colored by cortical pigmentation (Mayer, 1952). The interparietal is composed of a variable number of bones; there is one bone present in 78.6% of specimens, two bones in 9.5%, three bones in 2.4%, no interparietal in 7.1%, and the bone is aberrant in 2.4% of *D. venustus* (Beer, 1965). Visceral measurements (in mm) are: length of large intestine, 374; length of small intestine, 207; percent of small to large intestine, 55.4 (Setzer, 1949). Mean measurements of the baculum (in mm) are: length, 10.35; height of base, 1.55; and width of base, 1.38 (Best and Schnell, 1974).

When *D. venustus* has water available ad lib., evaporative water loss through the skin and respiratory tract is 0.50 mg of water/ml of oxygen consumed while subsisting on air-dry (8-9% water) seeds. When subsisting only on air-dry seeds (without water ad lib.) for ca. 1 month, pulmocutaneous water loss decreases to 0.34 mg of water/ml of oxygen and in 5.5 weeks body mass declines 34% (range, 29-38%). After restoration of free water, *D. venustus*



FIG. 1. A male *Dipodomys venustus* from near Felton, Santa Cruz Co., California.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Dipodomys venustus* (male, from Fremont Peak, Monterey Co., California; Los Angeles County Museum of Natural History 7224). Greatest length of cranium is 35.3 mm. Photographs by T. H. Henry.

returns to 95% (93–96%) of initial body mass within 25 days (Church, 1969).

Progressive emaciation characterizes water-deprived *D. venustus*. There is pronounced loss of flesh along its back and hindquarters and the eyes, which normally protrude, become sunken and, eventually, partially close. Its decreased pulmocutaneous water output when water intake is curtailed seems an incomplete compensation for occasional natural drought, since it loses mass on a dry diet. *D. venustus* survives better during water deprivation than some sympatric rodents and evidently requires exogenous water, unlike certain desert-inhabiting dipodomys. The Santa Cruz kangaroo rat is primitive with respect to its water dependence, and this may be partly the cause for restriction of this species to mesic habitats (Church, 1969).

ONTOGENY AND REPRODUCTION. One or two litters of two to four young each are produced each year (Jameson and Peeters, 1988). A nest excavated on 31 May contained one young that was too small to run; it squirmed to escape and made a suckling noise (Hawbecker, 1940).

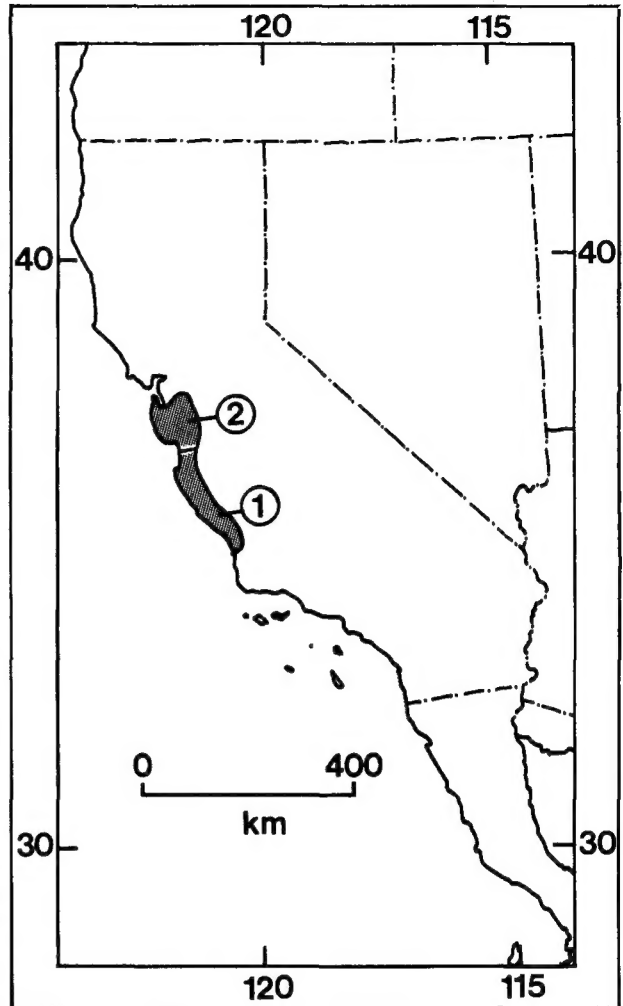


FIG. 3. Distribution of *Dipodomys venustus* in western North America (Hall, 1981): 1, *D. v. sanctiluciae*; 2, *D. v. venustus*.

ECOLOGY. *Dipodomys venustus* lives in cool, maritime areas where annual rainfall is ca. 75 cm. Although the precipitation is seasonal (82% occurs from November through March), the dryness of the long, rainless summer and autumn is tempered by frequent fogs and proximity to the ocean. These general moisture conditions and moderate temperatures present *D. venustus* with a relatively mild, moist habitat (Church, 1969).



FIG. 4. Habitat occupied by *Dipodomys venustus* near Felton, Santa Cruz Co., California.

In Santa Cruz County, California (Fig. 4), *D. venustus* occurs on sandy, well-drained, and deep soils that have been disturbed by human activity. Perennial plants that originally covered the area are *Adenostoma fasciculatum*, *Salvia mellifera*, *Arctostaphylos tomentosa*, *Ceanothus cuneatus*, *Baccharis pilularis*, *Sequoia sempervirens*, *Pseudotsuga taxifolia*, *Arbutus menziesii*, and *Lithocarpus densiflorus*. Annual vegetation included *Bromus rigidus*, *Rumex acetosella*, and *Heterotheca grandiflora* (Hawbecker, 1940).

Burrows are located in open, abandoned agricultural land. Burrows are on well-drained soils and consist of a main runway, a few blind side branches, and a nest and food caches. One burrow was 2.4 m in length with a 1.4-m side branch, five caches, and a nest. Burrows at least 2 years old are no more complex than those only months old. The lack of protection offered by such a simple main burrow system seems to be partially offset because each animal apparently has several supplementary burrows not too closely associated with the main one. Often, the two main burrow openings and one or both of the auxiliary burrow openings are under weeds or shrubs. The supplementary burrows are simple, often unbranched runways without nests, caches, or sidepockets. They are left open at all times. On the surface, the two burrow types can be distinguished because the main burrow openings usually are plugged, while the subsidiary burrow openings always are open. Burrows are 5–50 cm below the ground surface, except where *D. venustus* occupies burrows of *Thomomys*. When disturbed, they will break out through one of the side branches of their burrow that ends near the surface and go directly to another opening. During the rainy period, burrows are damp because the rain soaks into the ground to a depth of 1.5 m (Hawbecker, 1940).

Burrows are absent from orchards and cultivated areas. Even light harrowing completely destroys the relatively shallow burrows. Where cultivation ceases for a year, *D. venustus* invades and digs burrows. However, *D. venustus* invades permanent contour ditches or any type of earth structure whose surface is not cultivated and extends its workings along the berms far out into the orchard. Such workings soon honeycomb the ditch or structure and weaken it to such an extent that it collapses (Hawbecker, 1940).

The nest cavity usually is lower than the rest of the burrow and filled with seed coats of *B. rigidus* and chaff from *H. grandiflora*. The nest often contains live insects such as crickets and dung beetles along with the Santa Cruz kangaroo rat (Hawbecker, 1940).

The diet is made up almost entirely by seeds of annuals, as determined by cheekpouch contents, underground caches, and surface caches. The most common food is the achene of *H. grandiflora*. This seed, with the pappus attached, is stored in great quantities. One or two underground caches, containing up to 3,145 cm³ of this species, were found in each burrow examined in December. The next most common food is *B. rigidus*. Other species (*R. acetosella*, *Medicago hispida*, and *Anagallis arvensis*) occur infrequently (Hawbecker, 1940).

Surface caches generally are 10 cm deep and ca. 5 cm in diameter. They usually are grouped more or less fanwise about the mouth of the burrow, but often are found singly at some distance from any burrow. These caches are not found at the subsidiary burrows. Seeds for some of these caches are carried up to 50 m from the source. Caching occurs during the summer and autumn when seeds ripen and fall (Hawbecker, 1940).

Traps baited with rolled oats are occupied or sprung and the bait is removed. Some green material is used as food, as one burrow contained a number of green heads of *R. acetosella* and several animals had *M. hispida* in their cheekpouches in March. Except for a little debris, only mature seed or seed husks are in the caches. In captivity, *D. venustus* eats commercial seed of oats, rye, barley, and vetch in preference to green material such as cabbage, lettuce, grass, or root vegetables (Hawbecker, 1940). Though *D. venustus* will not readily take water from drinking tubes, it will maintain body mass and good health while subsisting on the water in carrots (Church, 1969).

Santa Cruz kangaroo rats occur in the same habitat as *Neotoma fuscipes* (Grinnell, 1933). Though *D. venustus* occurred in moderate numbers nearby, none were found in pellets of the barn owl (*Tyto alba*; Hawbecker, 1945). Potential predators include *Canis latrans*, *Felis rufus*, and *F. silvestris* (Hawbecker, 1940).

Internal parasites of *D. venustus* include the flagellated protozoan *Tritrichomonas muris* (Kirby and Honigberg, 1949), an unidentified coccidian protozoan of the genus *Eimeria* (Hill and Best, 1985), and the cestode *Catenotaenia linsdalei* (Voge, 1948). Ectoparasites include: the chiggers *Acomatacarus hirsutus*, *Euschön-*

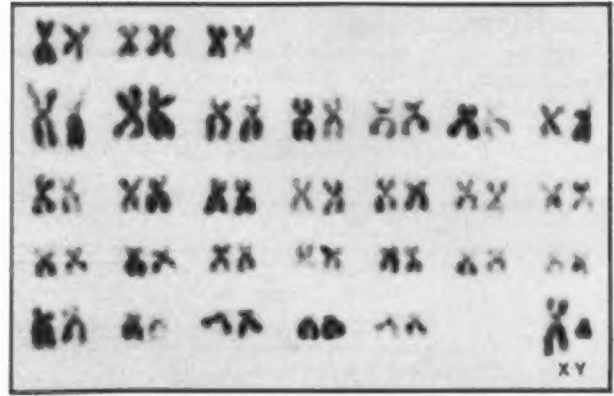


FIG. 5. Karyotype of a male *Dipodomys venustus* from Santa Clara Co., California (Hsu and Benirschke, 1975).

gastia criceticola, *E. radfordi*, *E. romola*, and *Trombicula californica* (Brennan and Jones, 1954); the listrophorid mites *Geomylichus texanus* and *G. californicus* (Fain et al., 1988); the laelapid mites *Androlaelaps fahrenheitsi*, *Eubrachyla elaps circularis*, *Ischyropoda armatus*, and *Echinonyssus incomptis*; the amero-seiid mite *Sertitympanum contiguum* (Thomas et al., 1991); the fleas *Meringis cummingi*, *Carteretta carteri*, *Diamanus montanus*, *Anomiopsyllus congruens*, *Peromyscopsylla hesperomys* (Linsdale and Davis, 1956), *Atheropsylla bakeri* (Stewart, 1940), and *Oropsylla aridis* (Traub et al., 1983); and the ticks *Dermacentor occidentalis* (Furman and Loomis, 1984) and *Ixodes pacificus* (Thomas et al., 1991).

GENETICS. The diploid number of chromosomes is 60 (Fig. 5) and the fundamental number of chromosome arms is 116. There are 3 metacentric autosomes, 21 submetacentrics, and 5 subtelocentrics; the X chromosome is submetacentric, and the Y chromosome is acrocentric (Stock, 1974). The proportion of DNA buoyant density fractions in neutral cesium chloride differs from other species of *Dipodomys*. *D. venustus* and other kangaroo rats, except *D. nitratoides*, have four fractions (Hatch et al., 1976). These density fractions are 1.713, 1.707, 1.702, and 1.698 g/ml (Hatch and Mazrimas, 1977).

REMARKS. The taxonomic relationships among *D. agilis*, *D. elephantinus*, and *D. venustus* are uncertain. Grinnell (1922) pointed out that, in some morphologic respects, *D. venustus* approached *D. elephantinus*, suggesting the latter is just one of a series of recently evolved races of *D. venustus*. He speculated that intergradation may occur to the north along the Gabilan Range in coastal California, whereby *D. elephantinus* would merge geographically with *D. venustus*. However, he noted that the flaring nasals of *D. elephantinus* distinguished it from *D. venustus* and all other *Dipodomys*. Best (1986) reported that some *D. venustus* also have flaring nasals. Additionally, Hall (1981) indicated that *D. elephantinus* is closely related to and possibly only subspecifically distinct from *D. venustus*. Likewise, comments in Honacki et al. (1982) indicate a questionable relationship between *D. elephantinus* and *D. venustus* and further suggest they may be conspecific with *D. agilis*. Hall (1981) pointed out the resemblance in width of the maxillary processes of the zygomatic arches of the skull between *D. agilis* and *D. venustus*, and speculated they eventually may be found to be only subspecifically distinct.

Grinnell (1921) placed *D. venustus* in the *agilis* group with *D. agilis* and *D. elephantinus*. Subsequent studies to elucidate relationships between *D. venustus* and other species of *Dipodomys* have used: skeletal and visceral measurements (closest affinities are with *D. heermanni*, *D. agilis*, *D. ingens*, and *D. elephantinus*; Setzer, 1949); field experience and chromosomes (*D. agilis* and *D. elephantinus*; Lidicker, 1960; Stock, 1974); bacula (*D. microps*, *D. agilis*, *D. compactus*, and *D. elephantinus*; Best and Schnell, 1974); and phenetic analyses of cranial and skeletal characters (*D. elephantinus*; Best, in press; Schnell et al., 1978).

Dipodomys is from the Greek words *di* (two), *podos* (foot), and *mys* (mouse) that refer to its enlarged hind feet and bipedal mode of locomotion. The name *venustus* is Latin and means charming or elegant (Jaeger, 1955).

B. Owen prepared Fig. 3. H. Bart, G. D. Baumgardner, R. S. Lishak, L. C. Wit, and an anonymous reviewer critically evaluated an early draft of the manuscript. This is journal article no. 15-902631P of the Alabama Agricultural Experiment Station.

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